PHOTOSYNTHETIC PERFORMANCE AND PRODUCTIVITY OF PHYTOPLANKTON IN THE SOUTHERN OCEAN

by

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for the degree of Doctor of Philosophy

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I declare that this thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text of the thesis, nor does the thesis contains any material that infringes copyright.

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Abstract

Marine phytoplankton account for approximately half of global primary production, an amount equivalent to their terrestrial counterpart. These short-lived organisms, with turnover rates between one and three weeks, support nearly all life in the ocean and have a profound effect on global biogeochemical cycles and climate. The connection between marine phytoplankton and climate is intimate and changes to either will profoundly affect the other. Over the years, due to high operational costs and distance from major human settlements, the Southern Ocean has been the least studied ocean, despite its significance in the distribution of nutrients to the world oceans, especially the lower latitudes, and controlling global climate. In order to capture the response of the phytoplankton to environmental change across the vast Southern Ocean, a method with high spatio-temporal resolution is desirable. By focusing on the Australian sector of the Southern Ocean, this dissertation examines the productivity and physiology of natural phytoplankton communities *in situ* using the fast repetition rate (FRR) fluorometry technique.

The FRR fluorometry technique was used to derive direct estimation of *in situ* primary productivity in the Southern Ocean during the SAZ-Sense (Sub-Antarctic Zone Sensitivity to Environmental Change) voyage in Jan-Feb 2007. A statistically significant correlation between FRR- and ^{14}C-derived primary production was observed ($r^2 = 0.85$, slope = 1.23±0.05, $p < 0.01$, $n = 85$) but the relationship between the methods differed vertically and spatially, mainly due to the effect of non-photochemical quenching under high irradiance. This indicates the FRR fluorometry technique can be used to determine *in situ* primary productivity in the Southern Ocean but care should be taken in the interpretation of the data.

In addition to the primary production measurements, the photosynthetic performance of phytoplankton was investigated to provide a better understanding of how natural phytoplankton communities acclimate to different environmental variables, especially in the iron-replete Subantarctic Zone (SAZ) and iron-depleted Polar Frontal Zone (PFZ). High effective

photochemical efficiency of photosystem II ($F'_q/F'_m > 0.4$), maximum photosynthesis rate (P^B_{max}), light-saturation intensity (E_k), maximum rate of photosynthetic electron transport ($1/\tau_{PSII}$), and low photoprotective pigment concentrations observed in the SAZ correspond to high chlorophyll *a* and iron concentrations. In contrast, phytoplankton in the PFZ exhibits low F'_q/F'_m (~ 0.2) and high concentrations of photoprotective pigments under low light environment. Strong negative relationships between iron, temperature, and photoprotective pigments demonstrate that cells were producing more photoproctive pigments under low temperature and iron conditions, and are responsible for the low biomass and low productivity measured in the PFZ.

FRR fluorometry data from 31 transects collected aboard MV I'Astrolabe between 2002 and 2009, were used to assess the photosynthetic performance of phytoplankton along a repeated transect from Hobart (42.8°S, 147.3°E) to the French Antarctic station, Dumont d'Urville (66°S, 140°E). The maximum photochemical efficiency of photosystem II (F_v/F_m) values were high in the Subtropical Zone and water close to the Antarctic continent, but low in the PFZ. Spring F_v/F_m were higher than other seasons, suggesting higher nutrient supply. High F_v/F_m observed in the Subtropical Zone and Antarctic Zone is consistent with moderate to high iron concentrations in these regions. Overall, phytoplankton photophysiology in the Southern Ocean is governed by nutrient distributions, especially iron, which are affected by atmospheric and oceanic physical processes.

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Statement of Co-Authorship

The following people contributed to the publication of the work undertaken as part of this thesis:

Paper 1/Chapter 2 (*Assessing Sub-Antarctic Zone primary productivity from fast repetition rate fluorometry*):

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- Andrew McMinn (6%)
- F. Brian Griffiths (4%)
- Karen J. Westwood (3%)
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Paper 2/Chapter 3 (*Dynamic influences of iron and temperature on phytoplankton photophysiology in the changing Sub-Antarctic Zone*):

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Brian Griffiths and Peter Strutton assisted with technical and conceptual aspects of the papers, as well as document preparation.

Karen Westwood, Simon Wright, and Lesley Clementson provided data and assisted in document preparation.

Ernesto Molina, Jason Webb, and Rick van den Enden provided assistance in data collection.

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Chapter 1

Introduction

1.1 Marine primary producers

The emergence of phytoplankton more than 3 billion years ago altered the way our planet behaves and has had a profound effect on atmospheric chemistry and global climate. The relationship between photosynthetic organisms and global biogeochemical cycles is highly interlinked (*Falkowski and Raven*, 2007). The habitability of our planet depends on marine primary producers, where they contribute approximately 50% of global primary production, support nearly all life in the oceans and play a key role in the interlocking climate and biogeochemical systems.

If we are to fully understand the Earth system, it is important to be able to obtain accurate and precise estimates of the primary productivity of the oceans. The aggregate biomass of aquatic primary producers amounts to less than 1% of the total plant biomass on Earth (*Falkowski*, 1994). More than 95% of the carbon fixation in the oceans is the result of the photosynthetic activity of single-celled algae, the phytoplankton. Phytoplankton collectively fixes about 45 gigatons of organic carbon annually (*Falkowski et al.*, 1998), which is equivalent in magnitude to global terrestrial primary production (*Behrenfeld et al.*, 2001; *Cramer et al.*, 2001). The turnover time of plants in marine ecosystems is about 0.02-0.06 years compared to 9-20 years in terrestrial ecosystems (*Falkowski and Raven*, 2007). Changes in the oceanic primary production, linked to changes in the network of global biogeochemical cycles, can strongly influence atmospheric CO_2 on geological time scales. Understanding the changes in ocean primary productivity will help explain how oceanic biota responded to and are affected by natural climatic variability in the geological past, and how they will respond to anthropogenically influenced changes in coming decades (*Falkowski et al.*, 1998).

1.2 The Southern Ocean

The Southern Ocean, which comprises approximately 10% of the world's oceans, is a major carbon sink for atmospheric CO_2 and plays an important role in controlling global climate. It also provides a unique environment that hosts a huge variety of marine organisms from single-celled phytoplankton to the largest mammals on Earth. The surface waters of the Southern Ocean are predicted to significantly change in response to climate change (*Sarmiento et al.*, 1998). Climate-driven atmospheric and oceanic changes are changing the mixing rates of the ocean and thus modifying the nutrient supplies that are required for photosynthesis. These changes will affect phytoplankton species composition, dynamics and growth rates in many ways. Changes in oceanic phytoplankton communities will lead to changes in marine food webs and strongly influence the ability of Southern Ocean to absorb atmospheric CO_2.

The Southern Ocean is characterised by dramatic gradients in physical and chemical properties, where, for example, sea surface temperatures can vary by up to 10 °C between its northern and southern boundaries (*Rintoul and Trull*, 2001). The hydrographic properties of the Southern Ocean are also characterized by extreme seasonal variability. This large variability makes the Southern Ocean a highly complex oceanographic region (*Rintoul and Trull*, 2001). Thus, marine organisms living in the Southern Ocean are exposed to these extreme environmental conditions where seawater temperature ranges from subzero to 20 °C. For phytoplankton, living in a such challenging environments requires fine tuning of their photosynthetic apparatus. The general seasonal pattern of phytoplankton blooms in the Southern Ocean (north of the ice edge) begins with winter, where cooling and strong winds extend the thermocline and enhance mixing of the upper ocean allowing nutrients to be mixed to the surface. In spring, increased sunlight, stratification and high nutrients concentration resulting from winter mixing in the euphotic zone lead to phytoplankton blooms. Apart from the physical challenges, phytoplankton in most of the Southern Ocean are also suffer from iron limitation. The s of macronutrients such as nitrate and phosphate are in excess all year round making the Southern Ocean the largest of the three major high nutrient

low chlorophyll (HNLC) regions in contemporary oceans (*de Baar et al.*, 2005). Being the largest HNLC region, the Southern Ocean, has the greatest potential to affect atmospheric CO_2 concentration (*Sarmiento and Orr*, 1991).

1.3 Measuring primary production

Traditionally, primary production has been measured chemically. One method uses the evolution of O_2 in light bottles, which allows the estimation of net primary productivity and community respiration (*del Giorgio and Williams*, 2005). Another common technique uses radioactive ^{14}C. The advantage of the ^{14}C technique over the O_2 technique is the much greater sensitivity which permits measurement at much lower biomass concentration (*del Giorgio and Williams*, 2005). Since the introduction of the ^{14}C method in 1952 (*Steemann-Nielsen*, 1952), this technique has become the most common method to estimate primary productivity in oceanographic research, due to its comparative simplicity and sensitivity (*del Giorgio and Williams*, 2005).

Despite the accuracy and sensitivity offered by both techniques, a common disadvantage is that both techniques require the samples be incubated in a container, which will create artefacts. The artefacts are associated with isolating natural phytoplankton assemblages and containing them in bottles (*Eppley*, 1980), and differentiating between net and gross photosynthesis (*Bender et al.*, 1987). Another disadvantage is that these techniques are time consuming and labourious and thus, limit the sampling rate. Furthermore, removal of phytoplankton from their natural environment limits the applicability of the results to the natural ecosystem. Assessment of primary production using satellite imagery has the potential to overcome some of these constraints and greatly improves spatial and temporal resolution (*Behrenfeld and Falkowski*, 1997). However, verification of these estimations with *in situ* measurements is always needed particularly at higher spatial and temporal resolution.

1.4 Fast repetition rate fluorometry

In situ, variable fluorescence-based measurements of phytoplankton photosynthesis potentially overcome many of the problems (e.g. artefacts from bottle incubation, labour intensive and time consuming) (*Kolber and Falkowski*, 1993). Variable fluorescence techniques provide valuable information of phytoplankton physiology in an instantaneous and *in situ* manner without the complication of artefacts from bottle incubations. One of the types of fluorometer that utilize this technique is the fast repetition rate (FRR) fluorometer (Fig. 1.1) (*Kolber et al.*, 1998).

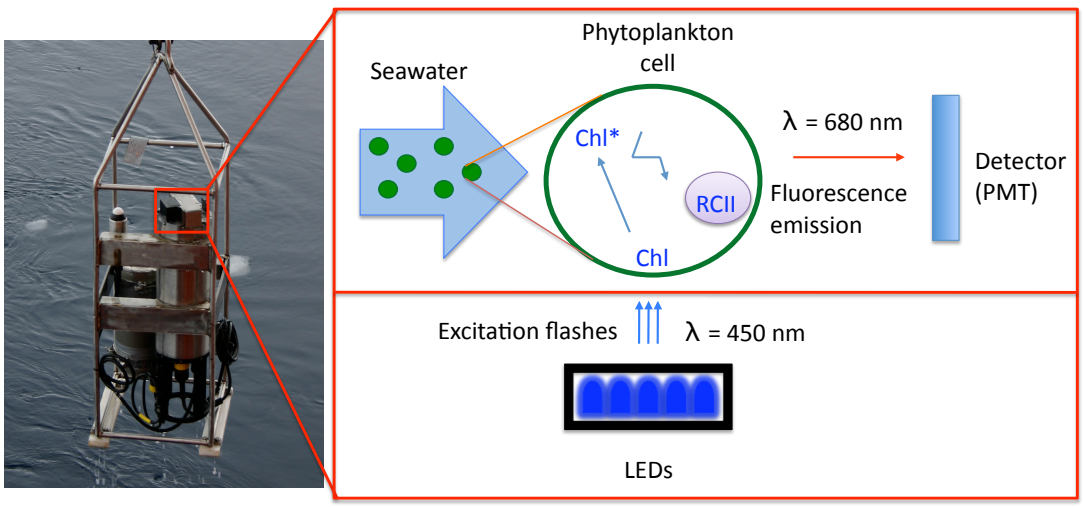

Figure 1.1: Fast repetition rate fluorometer during deployment mode and measuring technique. The dual (light and dark) optical chambers contain series of blue light-emiting-diodes that provide subsaturating excitation flashes at 200 kHz repetition rate and fluorescence released from excited chlorophyll pigments will be detected by highly sensitive photomultiplier tube.

Using subsaturating (peak energy up to 0.03 mol photons $m^{-2}s^{-1}$) excitation flashlets, the FRR fluorometer interrogate photosynthetic properties from light harvesting by photo-

system II (PSII) antennae to oxidation of the plastoquinone (PQ) and measures the initial (F_o), and maximal (F_m) fluorescence yields resulting from the progressive closure of PSII reaction centres and derives photosynthetic parameters such as the maximum photochemical efficiency of PSII, F_v/F_m, and effective absorption cross-section of PSII, σ_{PSII} (Fig. 1.2). FRR fluorescence yields were measured using a flash sequence consisting of a series of 100 subsaturation flashlets (1.1 μs flash duration and 2.8 μs inter flash period) (Fig. 1.3).

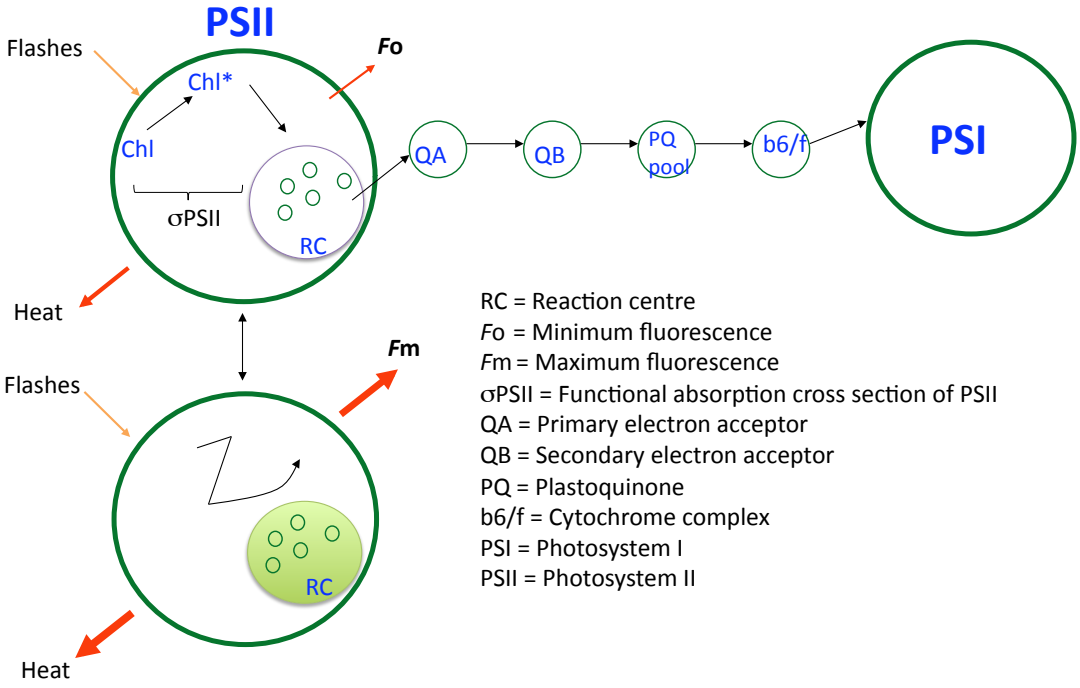

Figure 1.2: Simplified illustration of photosystem II. Light-harvesting pigments such as chlorophyll get excited after absorbing light energy (flashes). The absorbed light energy can then migrate to a reaction centre. If the reaction centre is open, minimum fluorescence F_o is released. If, at the instant of the photon absorption, the reaction centre is closed, the absorbed energy can be reradiated as fluorescence, increasing the fluorescence yield to F_m. Modified from (*Kolber and Falkowski*, 1993)

One of the major advantage of FRR fluorometry technique is the rapid measurement rate of up to 1 second. This allows the photosynthetic parameters of the changing phytoplankton community to be monitored in near real time. The photosynthetic photosynthetic parameters, such as the maximum photochemical efficiency of PSII (F_v/F_m) and effective

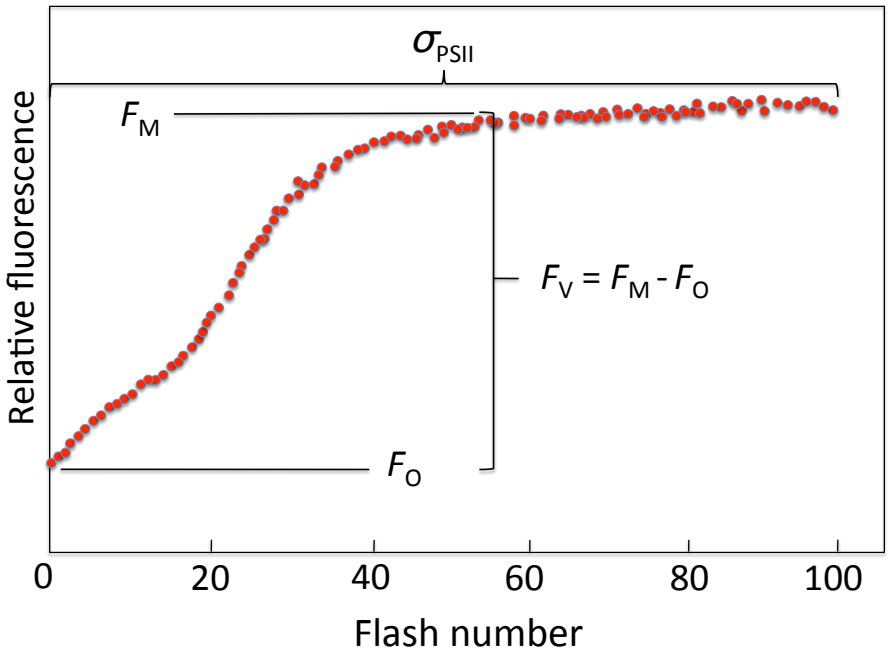

Figure 1.3: Excitation flashes and relative fluorescence emission during a fast repetition rate fluorometry protocol. The excitation flashes consist of 100 subsaturation flashlets at 1.1 μs flash duration and 2.8 μs inter flash period.

absorption cross-section of PSII (σ_{PSII}) are sensitive to environmental variables such as light and nutrients. For instance, a decline in $F_{\mathrm{v}}/F_{\mathrm{m}}$ has been used as an indication of iron deficiency (*Behrenfeld et al.*, 1996) in phytoplankton cells, a trace metal known to strongly limit primary productivity in up to 30% in the world's ocean (*de Baar et al.*, 2005). In addition, when these photosynthetic parameters are combined with other environmental information, such as irradiance and biomass, estimation of primary production at fixed depths and continuous observations with a temporal resolution of seconds can be achieved (*Suggett et al.*, 2005). Thus, FRR fluorometry offers unique *in situ* information on the photosynthetic competence and productivity of phytoplankton at a high temporal and spatial resolution, with minimal artefacts and allows rapid and real-time detection of change in phytoplankton.

1.5 Thesis objectives

The principle aim of this thesis is to investigate the coupling between the biological, chemical and physical processes that govern the physiological response and primary productivity of phytoplankton in the Southern Ocean, based on *in situ* observations measured with a FRR fluorometer and other oceanographic instruments. The main research themes of this thesis are:

- to investigate the relationship between FRR- and ^{14}C-derived primary production in order to understand the reliability and applicability of FRR fluorometry to estimate primary productivity in the Southern Ocean.

- to assess how phytoplankton physiology in the Southern Ocean responds to the distinctive environmental variables.

- to investigate the seasonal and interannual variation in phytoplankton physiology in different water masses ranging from the subtropical to the polar waters.

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